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ORIGINAL PAPER

Predicting the distribution of cryptic species: the case of the spur-thighed tortoise in Andalusia (southern Iberian Peninsula)

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Abstract Some species are very difficult to observe in the wild, and some of these present an apparently incongruent distribution, as is the case of the spur-thighed tortoise *Testudo graeca* in the southern Iberian Peninsula. This species has a discontinuous distribution with two main reproductive areas: one in the contiguous provinces of Almeria and Murcia, and the other in Huelva province. Both populations are thought to maintain reproductive isolation. However, we present new records obtained from two areas (the provinces of Malaga and Cadiz) which are outside their previously known range. Malaga province and Cadiz province are located between the two traditional reproductive areas. The new records were based on 16 interviews with shepherds as well as information provided by three naturalists. The aim of this work was to analyze the spatial distribution of areas favourable to the spur-thighed tortoise in the southern Iberian Peninsula, using different models with the same group of variables but with a different number of records: known records, new records and a combination of them. We obtained a distribution model for the species in Andalusia consistent with all observations, which was related to climatic stability, climatic disturbances, and spatial situation. This model presented three main favourable areas: two are coincident with the two known nuclei, and the other is situated in the southern part of the region, in the contiguous provinces of Cadiz and Malaga. We conclude that it is important to consider all the observations in the distribution models because records outside the traditional reproductive areas can include other environmental characteristics appropriate for the species.

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Abbreviations

AUC	Area under the curve
CCR	Correct classification rate
F	Favourability function
FDR	False discovery rate
LEK	Local ecological knowledge
LR	Logistic regression
OGU	Operational geographical unit
P	Probability of occurrence
SDM	Species distribution modelling

Introduction

There is increasing interest in studies using species distribution models, mainly due to their use in conservation biology and for the identification of predicted changes in distributions according to future climate and land-use change scenarios (Real et al. 2009, 2010; Estrada et al. 2010, 2011; Márquez et al. 2011). In an elegant and unconventional paper, Lozier et al. (2009) modelled the potential distribution of the cryptic species Sasquatch (or Bigfoot) in western North America. These authors found a distribution very similar to that of the black bear *Ursus americanus* and concluded that many sightings of these cryptozoids may be cases of mistaken identification. In this context, some species are very difficult to observe in the wild and some of these present an apparently incongruent distribution, as is the case of the spur-thighed tortoise *Testudo graeca* in the southern Iberian Peninsula (Díaz-Paniagua and Andreu 2009).

The spur-thighed tortoise is a terrestrial tortoise species distributed throughout the southwestern Palearctic Region. Western populations are found on both sides of the Strait of Gibraltar (Álvarez et al. 2000). In this large region, as noted by Fritz et al. (2007), "*Spur-thighed tortoises occur under very different climatic and environmental conditions, ranging from a Mediterranean climate with mild, frost-free winters to an extreme continental steppe climate with severe winter frost*".

Currently, the spur-thighed tortoise has a discontinuous distribution in the Iberian Peninsula with two main reproductive areas which are 400 km apart: one in the contiguous provinces of Almeria and Murcia, and the other in Huelva province. Both populations are thought to maintain reproductive isolation (Andreu et al. 2000), and are completely integrated in the natural ecosystems (Díaz-Paniagua and Andreu 2009).

Recent studies suggest that the origin of the *T. graeca* complex was located in the Caucasus region, due to its current high diversity of subspecies and fossil records (Fritz et al. 2007). Moreover, fossil records exist for the spur-thighed tortoise in Morocco dating from the Pliocene and Paleolithic epochs (Fritz et al. 2007; Nespoulet et al. 2008). However, no tortoise fossils have been found in the southern Iberian Peninsula despite there being excellent fossil records of other species (Bailón 2001; Giménez-Casalduero et al. 2004; Morales-Pérez and Sanchis-Serra 2009). For this reason, many authors have suggested that the founder individuals of the current Spanish populations were introduced, or are the result of relatively recent transoceanic dispersal (Fritz et al. 2007, 2009). Historical records exist of the spur-thighed tortoise being introduced in Majorca

(Balearic Islands) (Mayol 1985), as well as Moroccan individuals being introduced very recently (between 1948 and 1954) in the Coto de Doñana (Huelva, Spain) (Andreu et al. 2000), although this species has been recorded in the Coto de Doñana at least since the 18th century, when Friar Enrique Florez described it in his "Catálogo de aves del coto" (Catalogue of Birds of the Coto) (Andreu et al. 2000). Moreover, Álvarez et al. (2000) found one shared haplotype between southern Iberian Peninsula populations and some eastern Moroccan specimens. However, some authors have suggested that Iberian populations could be the relic of a wide distribution in Eurasia, and that the colonization movement took place from Iberia to the North of Africa (Loveridge and Williams 1957, in Díaz-Paniagua and Andreu 2009). In a recent paper based on genetic analysis, Fritz et al. (2009) suggested that Spanish *T. graeca* are not clearly differentiated from the North African lineages, and that Iberian populations originated from transoceanic dispersal in historic or prehistoric times. In any case, the species is considered to be at least naturalised in the Iberian Peninsula (Díaz-Paniagua and Andreu 2009), and is a species of high conservation concern as it endangered in Spain due to the contraction of its distribution range, among other causes (Andreu 2004).

In this context, the fact that Spanish spur-thighed tortoise populations present a discontinuous distribution is a conservation concern. The main threats for the species are habitat loss and fragmentation, changes in traditional land use, and the capture of adult specimens as pets (Giménez-Casalduero et al. 2004). In addition, the deliberate capture of wild specimens as pets and their subsequent non-controlled release in other parts of their distribution area is a particular problem for threatened species (Giménez-Casalduero et al. 2004).

Báez et al. (2007) found one specimen of a spur-thighed tortoise by chance in the wild, in Malaga province, which lies between the two large reproductive areas in the southern Iberian Peninsula. This possibly involved a non-controlled release. However, the specimen showed normal feeding patterns. This raised the question of whether this distribution pattern is the result of a previously established, even distribution pattern that deteriorated leaving behind relic nuclei, or, on the contrary, this is the result of differential selection of the habitat by the species after being randomly, but deliberately, introduced. We used the local ecological knowledge (LEK) approach to obtain new records of the species, and species distribution modelling (SDM) to test whether the new records could be combined with those of the two separate distribution nuclei in one coherent ecogeographical model. The latter possibility would indicate that the new reports correspond either to rare records of a cryptic ancient distribution pattern or to records of a new but naturalised distribution pattern. We used diverse models with the same group of variables but with different numbers of records: known records, new ones and a combination of them. We used the records of specimens observed in the wild in the two large reproductive areas, in combination and separately. We also used the records of specimens found between the two large reproductive areas and identified new areas favourable to non-controlled release. The final aim was to achieve a distribution model consistent with all observations representing favourable areas that could be used as bridges between the two isolated populations.

Methods

Study area and operational geographical units

Andalusia is a southern region of mainland Spain and covers 87600 km^2. It is one of the 17 Spanish autonomous regions and is divided into eight administrative provinces (Fig. 1).

Fig. 1 Location of Andalusia (*shaded grey*) in the Iberian Peninsula. The borders of its eight provinces are shown and the provinces mentioned in the text are named

The climate is Mediterranean with a marked precipitation gradient, ranging from 170 to more than 1800 mm/year. The elevation gradient is also large, ranging from sea level to almost 3,500 m.a.s.l. Climatic and orographic heterogeneity results in high habitat diversity in Andalusia. We selected the Andalusian region for this study due to the special political division of Spain that allows the region to be an independent management unit. Conservation policy rights in Spain, including the right to reintroduce wildlife, are devolved to the autonomous regions. In addition, any possible bridge between the two populations of the species must be included in this region. This region is part of one of the biodiversity hotspots defined by Myers et al. (2000), and covers an area similar to European countries such as Hungary, Portugal or Austria.

The operational geographical unit (OGU) was the 10×10 km^2 UTM. The map of 10×10 km^2 UTM for Andalusia was obtained by superimposing the digital outline of Andalusia on the digital map of UTM^2 for the Iberian Peninsula using Cartalinx software (Estrada et al. 2008). The presence or absence of the spur-thighed tortoise was mapped onto these OGU, and the variables used for the distribution models were introduced.

Data collection

The basic data source for the presence or absence of the spur-thighed tortoise was the second edition of the *Atlas y Libro Rojo de los Anfibios y Reptiles de España* (Pleguezuelos et al. 2004). As LEK has been shown to be effective in detecting the distribution and abundance of this species in southern Spain (Anadón et al. 2009, 2010), and in order to know if the specimen seen by Báez et al. (2007) co-occurred with other individuals, we placed an advertisement in a popular national magazine specialising in nature and the environment (*Quercus*), asking naturalists to report any sightings of spur-thighed tortoise in Andalusia (see Báez and Torreblanca 2007, 2008). Subsequently, we conducted interviews in the areas where new records had been reported in response to the advertisement. We interviewed shepherds, first performing a semi-structured interview with the people chosen for the interview. Shepherds were selected by following a few simple criteria:

adults over 50 years old, with obvious signs (dress and accent) of being a worker or resident in the area, and with excellent knowledge of the area. They were asked simple questions: "Have you seen a tortoise in the wild?", "Could you describe it?", and "When was the last time you saw one?" These questions made it possible to distinguish between pond turtles and the genus *Testudo*, although during the interview it was practically impossible to differentiate between the two species of the genus *Testudo* found in the Iberian Peninsula. The two species (spur-thighed tortoise and Hermann's tortoise *T. hermanni*) have an allopatric distribution in the Iberian Peninsula, with the populations of Hermann's tortoise being concentrated in the northeastern Iberian Peninsula. Thus, it was assumed that the sightings in Andalusia were of spur-thighed tortoises.

The resolution scale was 10×10 km^2 UTM cells for the atlas. The records provided by naturalists in response to the advertisement were accompanied by the GPS data at an accuracy of 1×1 km, whereas the presence locations derived from the interviews, although approximate, were well defined. We then joined these presence points to the 10×10 km^2 UTM grid to construct the model at this spatial resolution.

Modelling method

Our aim was to identify the spatial distribution of the spur-thighed tortoise in Andalusia. Thus, we used different models with the same set of variables, with a different number of records and applied the favourability function. First, we selected the subset of variables significantly associated with the distribution of the species. We then applied the favourability function to the different groups of records and calculated the effect of including each model in the other models attempting to select the one that indicated maximum variability. Finally, to facilitate understanding of this model we performed a variation partitioning procedure. These steps are described below.

The following ecogeographic factors were taken into account when creating the model: geographic, topographic, water availability, energy resources, climatic stability, climatic disturbances, lithologic and anthropogenic. Each factor was represented by a set of macro-environmental variables (see Table 1). Variables had an initial resolution scale of 1 km^2 and we obtained the mean value of each variable in the 961 (10×10 km^2) UTM cells of Andalusia using the Idrisi Extract module.

To control for the increase in type I errors due to multiple tests (Benjamini and Hochberg 1995; García 2003), we performed a logistic regression of the species' presence or absence on each variable separately, and selected the subset of variables significantly associated with the distribution of the species, only accepting those variables that were significant under a false discovery rate (FDR) of $q < 0.05$ (Benjamini and Hochberg 1995). We then continued the modelling procedure on the subset of significant predictive variables.

In the last decade, we have witnessed an increase in predictive mathematical models, based on the occurrence of species in given areas. These models associate the geographic distribution of a given species with a set of ecogeographic variables (Bustamante 1997; Real et al. 2008). Binary logistic regression (LR) is a widely used statistical tool for these potential distribution models (see, for example, Bustamante 1997; Real et al. 2006). However, LR is sensitive to the presence/absence ratio, regardless of the goodness-of-fit of the model (Hosmer and Lemeshow 2000). Real et al. (2006) obtained a favourability function (F) based on a logistic regression model. This function identifies the areas that are environmentally favourable to the species, regardless of the presence/absence ratio. Favourability was easily calculated from the probability obtained from the LR according to the expression:

Table 1 Explanatory factors and variables used to model the distribution of the spur-thghed tortoise in Andalusia

Factors	Code	Variables
Spatial situation	Lati	Latitude (°N)[a]
	Long	Longitude (°E)[a]
Topography	Alti	Mean altitude (m)[b]
	Slop	Slope (°) (calculated from Alti)
	HuJan	Mean relative air humidity in January at 07:00 (%)[c]
Lithology	Perm	Soil permeability[a]
Climatic stability	DPre	Mean annual number of days with precipitation $\geq$0.1 mm[c]
	HRan	Annual relative air humidity range (%)(= |HuJan-HuJul|)
	TRan	Annual temperature range (°C)(= TJul–TJan)
	PET	Mean annual potential evapotranspiration (mm)[c]
	PIrr	Pluviometric irregularity[c]
	ConI	Continentality index[c]
Energy availability	TJan	Mean temperature in January (°C)[c]
	TJul	Mean temperature in July (°C)[c]
	Temp	Mean annual temperature (°C)[c]
	DFro	Mean annual number of frost days (minimum temperature $\leq$0°C)[c]
	Inso	Mean annual insolation (h/year)[c]
	SRad	Mean annual solar radiation ((kWh/m^2/day)*100)[c]
Water availability	HumI	Humidity index[c]
	DSno	Mean annual number of snowy days[c]
	HuJul	Mean relative air humidity in July at 07:00 (%)[c]
	ROff	Mean annual runoff (mm)[d]
	Prec	Mean annual precipitation (mm)[c]
Disturbances	MP24	Maximum precipitation in 24 h (mm)[c]
	RMP	Relative maximum precipitation (= MP24/Prec)
Productivity	AET	Mean annual actual evapotranspiration (mm) [= min (Prec, PET)]
Human activity	DHi	Distance to the nearest highway (km)[a]
	Harb	Presence of passenger harbour with fast ferry connection with Morocco[e]
	U100	Distance to the nearest urban centre with more than 100,000 inhabitants (km)[a]
	U500	Distance to the nearest urban centre with more than 500,000 inhabitants (km)[a]

Data on the number of inhabitants in the urban centres were taken from the Instituto Nacional de Estadística, Spain (http://www.ine.es)

[a] IGN (1999)

[b] US Geological Survey (1996)

[c] Font (2000)

[d] IGME (1979)

[e] Andalusian Port Authority (http://www.eppa.es)

$$F = [P/(1-P)]/[(n1/n0) + (P/[1-P])]$$

where P is the probability of occurrence, n1 is the number of presences, and n0 is the number of absences.

We selected the favourability function because we were interested both in the explicative and the predictive outputs. Predictive maps obtained by LR are affected by prevalence; however, favourability values only indicate the environmental conditions which are appropriate for the species. We preferred the concept of favourability to that of suitability. Favourability is a concept which is implicit in that of probability and can be derived only from it. The favourability function assesses variations in the probability of an event occurring under certain local conditions in relation to the overall prevalence of the event, and there is only one way of obtaining favourability values from probabilities. Favourability values are thus interpretable in absolute terms, as they indicate how the probability of local presence differs from that expected by chance in the total study area. Favourability is different from suitability, which is a way of ranking local sites according to their capacity to hold the species, but is not related to probability. A direct interpretation of suitability values is not possible, since suitability scores are relative and therefore non-informative in absolute terms. This is why different techniques producing different suitability values can be used, but all the ways of obtaining favourability yield the same favourability values.

We used five favourability models with the same group of variables (Table 1) in a forward–backward stepwise procedure but with different numbers of records: a) a model using known records from Pleguezuelos et al. (2004) for both Almeria and Huelva (Model A); b) a model using records from Huelva (western Andalusia, Model B); c) a model using records from Almeria (eastern Andalusia, Model C); d) a model using only new records (Model D); and, e) a model using all the records (known and new ones, Model E). The total number of cells analyzed was always 961.

The F values do not indicate presence probability, but rather environmental favourability values. F is also a logistic function, and assumes values ranging from 0 to 1. The favourability function is related to fuzzy logic because the favourability value for a species in a cell can be interpreted as the degree of membership in the fuzzy set of areas favourable to the species. In this sense, the favourability function is the membership function, and the concepts of fuzzy logic can be applied to the resulting spatial analysis of the species (Estrada et al. 2008). We calculated the effect of including each model in the other models trying to select the one which indicated maximum variability by performing fuzzy inclusion:

$$\subset = \frac{c\,(F_1 \cap F_2)}{cF_1}$$

where cX is the cardinality of the corresponding X fuzzy set, that is, the sum of all the squares' favour abilities, F_i refers to the fuzzy set of favourable areas according to each model, $(F_1 \cap F_2)$ is the intersection between the two favourability models, that is the minimum favourability value for each square.

The goodness-of-fit of the final model (using all the records) was assessed using the Hosmer and Lemeshow test. The discriminatory power of the models was assessed by calculating their correct classification rate (CCR), sensitivity, and specificity, using the favourability value of $F = 0.5$ as classification threshold, and the area under the curve (AUC) of the receiver operating characteristic, which is independent of any favourability threshold (Hosmer and Lemeshow 2000).

To facilitate understanding of the complete model (Model E) and to explain the current and predicted distributions of the species, we grouped the variables included in the model into explanatory factors (Table 1). To take into account the combined effect of the variables affecting the distribution of the spur-thighed tortoise—which often results in an overlaid effect in space due to collinearity between them (Borcard et al. 1992; Legendre

1993)—we performed a variation partitioning procedure. This allows specifying how much of the variation of the complete model (Model E) was explained by the pure effect of each factor (R^2_{pi}) not affected by collinearity with other factors in the model, and which proportion was attributable to their shared and indistinguishable effect (Legendre 1993; Legendre and Legendre 1998; Muñoz and Real 2006). The part of the variation of the model explained by each factor (R^2_i), both exclusively and in combination with other factors, was obtained by using the squared value of the Spearman correlation coefficient between the values obtained in Model E and in a model based only on each factor. We used Spearman correlation because model outputs had non-normal frequency distributions. The pure effect of each factor (R^2_{pi}) was assessed by subtracting the variation explained by the other factors taken together from the variation explained by the complete explanatory model. The overlaid effect of two factors can be obtained by subtracting their pure effects from their combined effect ($R^2_{i+j} - (R^2_{pi} + R^2_{pj})$). The variation attributable to the combined effect of trios, quartets, etc., may be obtained similarly by subtraction (see Whittaker 1984; Legendre and Legendre 1998, pp. 532–534).

Results

Three naturalists responded to the advertisement placed in the magazine *Quercus* which produced five new records of the species in the provinces of Malaga and Cadiz. Photographs were available in all cases making it easy to identify the species. In this way, we had three different groups of records: Almeria, Huelva and Cadiz-Malaga. Almeria and Huelva were the two known nuclei (Pleguezuelos et al. 2004), and Cadiz-Malaga corresponded to the new records obtained from the responses of the naturalists.

A total of 16 interviews with shepherds were performed in the provinces of Malaga and Cadiz of which six resulted in positive reports. Thus, 37.5% of the respondents had seen specimens, which was far more than initially expected. Of note, three of the respondents claimed that tortoises were very common around private gardens along the coast of Marbella (Malaga, Spain), thus living in the semi-wild, although they assumed these specimens were brought from Morocco. Another two respondents, all over 60 years of age, claimed that these animals were frequent in the wild in the central area of Malaga province in the 1950s.

Using this information, a total of nine new squares (Table 2) were included as presences, complementing those established by Andreu (2004). Figure 2 shows presences and absences of the species, both known and new, in Andalusia.

Table 2 New records of the spur-thighed tortoise in Andalusia obtained in this study (result of the interviews and the responses of the naturalists)

UTM 10 × 10 km^2	Province
TE68	Cadiz
TE79	Cadiz
TF70	Cadiz
TF80	Cadiz
UF34	Malaga
UF44	Malaga
UF66	Malaga
UF77	Malaga
UF86	Malaga

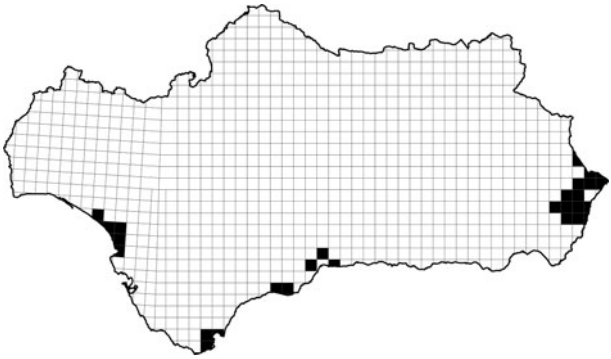

Fig. 2 Presences of the spur-thighed tortoise in each UTM 10×10 km^2 in Andalusia. Presences reported by Pleguezuelos et al. (2004) are located in Almeria and Huelva, and new records obtained in the present study in Cadiz and Malaga (see Fig. 1)

Figure 3 illustrates favourability models for the species using different presence records, while Table 3 shows the variables that form part of the models. The distribution of high favourability values using known records (Model A, Fig. 3a) approximately coincides with the records used to build the model. The same tendency is obtained when using records from Huelva or Almeria only (Models B and C, Fig. 3b, c). In contrast, the favourability model obtained with the new records (Model D, only nine presences) is larger than the other models and detects favourable areas in Cadiz-Malaga but also near the two known nuclei (Fig. 3d). The model built with all the records (Model E, Fig. 3e) presents three main nuclei with high favourability values which are more or less connected with lower favourability values.

The results of the fuzzy inclusion procedure are shown in Table 4. Different partial models are widely included in the complete one (Model E, built with all the records), with scores from 0.722 to 0.916.

The complete favourability model obtained (Model E) had outstanding discriminatory power according to the Hosmer and Lemeshow test (2000) (AUC = 0.971, sensitivity = 0.969, specificity = 0.889, CCR = 0.892), and includes 5 variables representing the following factors: climatic stability, climatic disturbances, and spatial situation (Table 3). There were no significant differences between the observed and the estimated expected frequencies, thus obtaining a high goodness-of-fit, according to the Hosmer and Lemeshow test ($\chi^2 = 0.614$, $P = 0.9997$, $gl = 8$).

The results of the variation partitioning of Model E are shown in Fig. 4. The pure influence of climatic stability variables explains most of the variation (almost 76%) and the pure influence of spatial situation accounts for a smaller (19.1%) proportion, whereas climatic disturbances explain less than 4% of the variation. A small proportion of the variation is explained by the overlaid effect of two of the factors, independently of the other factor. The combined effect of the variables climatic stability, spatial situation, and disturbance was negative.

Discussion

According to our results, the model for Almeria (Model C) did not explain the distribution of the species in Huelva, and vice versa (Fig. 3; Table 4). Moreover, the model obtained with the known distribution (Model A) did not predict the new records obtained in the present study. However, we have obtained a complete distribution model using all the

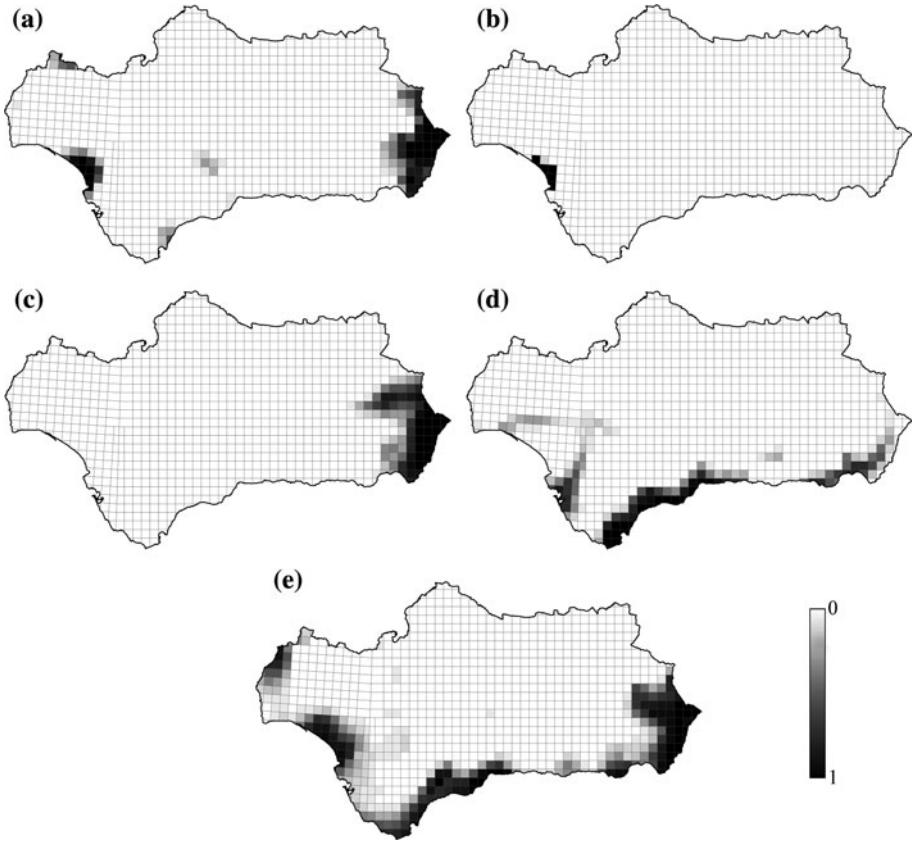

Fig. 3 Favourability values for the spur-thighed tortoise in each UTM 10 × 10 km^2 in Andalusia: **a** using known records from Pleguezuelos et al. (2004), for both Almeria and Huelva (model A); **b** using records for Huelva (model B); **c** using records for Almeria (model C); **d** using new records only (model D); and **e** using all the records (known and new ones, model E)

Table 3 Variables included in the favourability models and their coefficients in the logit function (*y*)

	y
Model A	−0.43DPre − 7.1 Long + 0.031U500 − 0.11PET + 2.2Temp + 2.6PIrr − 0.02Prec − 40.7
Model B	24.9SRad − 13.0U500 + 48.5HuJul − 40.4Lati − 13839.1
Model C	−0.14 DPre + 0.076U500 − 0.19DHi − 8.3
Model D	−1.4TRan − 0.33DHi + 0.007ROff + 19.0
Model E	−2.6TRa − 0.13DPre − 11.2RMP + 0.43PIrr + 5.7Lati − 182.6

The variables are ranked according to their order of entry in the models. Variables codes are the same as in Table 1. Records used in the favourability models: Model A, known records from Pleguezuelos et al. (2004) for both Almeria and Huelva; Model B, records from the west of Andalusia; Model C, records from the east of Andalusia; Model D, new records obtained in the present study; Model E both known and new records (see "Methods" for more details)

records (both new and known ones, Model E), implying that the recently recorded specimens did not have the stochastic distribution which would be expected according to random releases. This complete distribution model presents high environmental

Table 4 Inclusion values of the favourability models for the different groups of records

	E	A	B	C	D
E⊂	1	0.371	0.0457	0.312	0.36
A⊂	0.83	1	0.11	0.606	0.133
B⊂	0.916	0.982	1	0.00000144	0.00519
C⊂	0.81	0.705	0.000000187	1	0.134
D⊂	0.722	0.119	0.000519	0.103	1

"E ⊂ D" means the inclusion of Model E in Model D, i.e., the inclusion of the favourability model using all the records in the favourability model using only new records. Records used in the favourability models as in "Methods" and Table 3

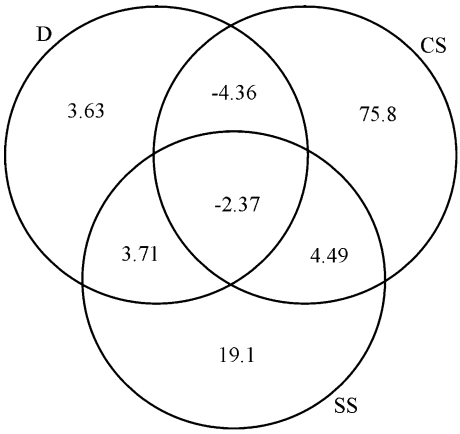

Fig. 4 Results of the variation partitioning of the complete model (performed with all records, model E). Values shown in the diagrams are the percentages of variation explained exclusively by *CS* climatic stability, *SS* spatial situation, *D* disturbances, and by the combined effect of these factors. *CS* includes *Tran*, *DPre*, and *PIrr*; *SS* includes *Lati*; and *D* is represented by *RMP*. Variable codes are the same as in Table 1

consistency. Lozier et al. (2009) noted the existence of a potential source of error in publicly available data that may affect the accuracy of species distribution models, mainly related to mistaken species identification. We consider that omitted observations, as could be the case of spur-thighed tortoise in southern Iberian Peninsula, may be another source of error if records outside the traditional reproductive areas are eliminated.

Three main areas were identified in the complete distribution model: i) the north and south of Huelva province; ii) some parts of Almeria province; and iii) the provinces of Malaga and Cadiz, which include the Gibraltar area and central Malaga province (Fig. 3e). Although these nuclei are not connected to each other, they form a continuum along the Andalusian coast. However, these three nuclei present very disparate landscapes. Whereas the north of Huelva and Cadiz-Malaga provinces are mountainous regions, the south of Huelva is a large wetland, and Almeria is mainly a desert area. Nevertheless, the species as a whole is currently spread over areas with different environmental conditions, which can be attributed to the high phenotypic plasticity of *T. graeca* and the fragmentation of a wider part distribution (Fritz et al. 2007). These results suggest that the distribution observed in the southern Iberian Peninsula could be the relic of a wider natural distribution. Although our Model E cannot be transferred to North Africa, because the predictor variables are not available in that area, the new favourable areas defined in the provinces of Malaga and Cadiz are the most similar to those of the distribution range of the species in Morocco, at least with regard to the geographically close Riff mountains, where *T. graeca* has a mainly western, northern and low elevation distribution (Real et al. 1997).

Regarding the variables that form part of the models (Table 3), human variables have been selected in all the partial models, whereas they were excluded from the complete one. In spatial models of introduced species it is common to obtain a pattern where variables related to human activity form part of the model (Muñoz and Real 2006; Real et al. 2008), but this was not the case of the complete spur-thighed tortoise model (Model E, Table 3). Thus, our results suggest that the disjunct distribution of *T. graeca* could be related to human activities, whereas the complete spur-thighed tortoise model could be related to the ecogeographical factors affecting the distribution of *T. graeca*.

In this regard, the environmental factor with highest explanatory power is climatic stability (few days with precipitation, highly pluviometric irregularities, and small variations in temperature) (Fig. 4), thus matching the environment expected for those ectothermic organisms which are not less demanding regarding resource availability. Anadón et al. (2006) also found that climate was the main limiting factor determining the distribution of the species in south-eastern Spain. The second factor with high explanatory power is spatial situation (latitude), thus indicating a historical distribution pattern of the species in the region.

Regarding conservation approaches, every year a number of tortoises are seized by the customs authorities at the frontier between Morocco and Spain. These are left in different animal shelters in Spain. A number of these individuals could die due to veterinary infections related to overcrowding (Schumacher 2006; Perez-Ibarra 2008). For wild populations of reptiles, the non-controlled release or escape of captive animals into the wild populations has been associated with population declines and the emergence of new diseases (Schumacher 2006). Moreover, pet owners may want to avoid using these shelters because they prefer a natural and pleasant area in which to release their pets. Thus, conservationists are interested in identifying suitable habitats for the species to provide better management and guide potential translocations of these specimens. The release of seized animals must be performed in places without contact with natural populations, thus avoiding possible contagious infections (Perez-Ibarra 2008). An example of this is the release of spur-thighed tortoises in 1987 by the Andalusian government in the Alcornocales Natural Park (Cadiz). It has been pointed out that insufficient data were available to indicate whether the introduction was successful (Andreu 2004), and thus whether the location was suitable for the species or not. According to our complete model, the animals were released in environments favourable to the species, and so it would be of interest to increase the sampling efforts in the area, due to the difficulty of finding them in the wild, to evaluate whether their introduction has been successful or not. In fact, if there is a population nucleus due to the release process, this would validate the favourability model proposed in this work.

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References

Álvarez Y, Mateo JA, Andreu AC et al (2000) Mitochondrial DNA haplotyping of *Testudo graeca* on both continental sides of the Straits of Gibraltar. J Hered 91:39–41

Anadón JD, Giménez A, Martínez M et al (2006) Factors determining the distribution of the spur-thighed tortoise in south-east Spain: a hierarchical approach. Ecography 29:339–346
Anadón JD, Giménez A, Ballestar R et al (2009) Evaluation of local ecological knowledge as a method for collecting extensive animal abundance data. Conserv Biol 23:617–625
Anadón JD, Giménez A, Ballestar R (2010) Linking local ecological knowledge and habitat modelling to predict absolute species abundance on large scales. Biodivers Conserv 19:1443–1454
Andreu AC (2004) *Testudo graeca* Linnaeus, 1758. Tortuga mora. In: Pleguezuelos JM, Márquez R, Lizana M (eds) Atlas y libro rojo de los anfibios y reptiles de España. Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid
Andreu AC, Díaz-Paniagua C, Keller C (2000) La tortuga mora (*Testudo graeca* L.) en Doñana. Monografías de Herpetología, Vol 5. Asociación Herpetológica Española, Barcelona
Báez JC, Torreblanca D (2007) Nuevos datos de la tortuga mora en Andalucía. Quercus 262:32–35
Báez JC, Torreblanca D (2008) Confirmada la presencia de tortuga mora en Málaga. Quercus 269:43–44
Báez JC, Báez M, Torreblanca D (2007) Presencia de la tortuga mora en la provincia de Málaga. Boletín de la Asoción Herpetológica Española 18:65
Bailón S (2001) Revisión de la asignación a *Testudo* cf. *graeca* del yacimiento del Pleistoceno superior de Cueva Horá (Darro, España). Revista Española de Herpetología 15:61–65
Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J R Stat Soc B 57:289–300
Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. Ecology 73:1045–1055
Bustamante J (1997) Predictive models for lesser kestrel Falco naumanni distribution, abundance and extinction in southern Spain. Biol Conserv 80:153–160
Díaz-Paniagua C, Andreu AC (2009) Tortuga mora –*Testudo graeca*. In: Carrascal LM, Salvador A (eds) Enciclopedia Virtual de los Vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid. Available from website: http://www.vertebradosibericos.org/searched on 20 May 2010
Estrada A, Real R, Vargas JM (2008) Using crisp and fuzzy modelling to identify favourability hotspots useful to perform gap analysis. Biodivers Conserv 17:857–871
Estrada A, Arroyo B, Márquez AL (2010) Possible changes in favourability areas for Montagu's and hen harriers in Spain according to climate change scenarios. Ardeola 57:123–128
Estrada A, Real R, Vargas JM (2011) Assessing coincidence between priority conservation areas for vertebrate groups in a Mediterranean hotspot. Biol Conserv 144:1120–1129
Font I (2000) Climatología de España y Portugal. Ediciones Universidad de Salamanca, Salamanca
Fritz U, Hundsdörfer AK, Široký P et al (2007) Phenotypic plasticity leads to incongruence between morphology-based taxonomy and genetic differentiation in western Palaearctic tortoises (*Testudo graeca* complex; Testudines, Testudinidae). Amphibia-Reptilia 28:97–121
Fritz U, Harris DJ, Soumia F et al (2009) Mitochondrial phylogeography of *Testudo graeca* in the Western Mediterranean: old complex divergence in North Africa and recent arrival in Europe. Amphibia-Reptilia 30:63–80
García LV (2003) Controlling the false discovery rate in ecological studies. Trends Ecol Evol 18:553–554
Giménez-Casalduero A, Esteve MA, Pérez-Ibarra I et al (2004) La tortuga mora en la región de Murcia. Conservación de una especie amenazada, Murcia
Hosmer DW, Lemeshow S (2000) Applied logistic regression, 2th edn. John Wiley and Sons Inc, New York
IGME (1979) Mapa hidrogeológico nacional. Explicación de los mapas de lluvia útil, de reconocimiento hidrogeológico y de síntesis de los sistemas acuíferos. Vol. 81, 2th edn. Instituto Geológico y Minero de España, Ministerio de Industria y Energía, Madrid
IGN (1999) Mapa de carreteras. Península Ibérica. Baleares y Canarias. Instituto Geográfico Nacional Ministerio de Fomento, Madrid
Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673
Legendre P, Legendre L (1998) Numerical ecology, 2nd edn. Elsevier Science, Amsterdam
Loveridge A, Williams EE (1957) Revision of the African tortoises and turtles of the suborder cryptodira. Bull Mus Comp Zool 115:163–557
Lozier JD, Aniello P, Hickerson MJ (2009) Predicting the distribution of Sasquatch in western North America: anything goes with ecological niche modelling. J Biogeogr 36(9):1623–1627
Márquez AL, Real R, Olivero J et al. (2011) Combining climate with other influential factors for modelling the impact of climate change on species distribution. Climatic Change. doi:10.1007/s10584-010-0010-8 (in press)
Mayol J (1985) Réptils i amfibis de les Balears. Moll, Palma de Mallorca

Morales-Pérez JV, Sanchis-Serra A (2009) The quaternary fossil record of the genus *Testudo* in the Iberian Peninsula. Archaeological implications and diachronic distribution in the Western Mediterranean. J Archaeol Sci 36:1152–1162

Muñoz AR, Real R (2006) Assessing the potential range expansion of the exotic monk parakeet in Spain. Divers Distrib 12:656–665

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nespoulet R, El Hajraoui MA, Amani F et al (2008) Palaeolithic and neolithic occupations in the témara region (rabat, morocco): recent data on hominin contexts and behaviour. Afr Archaeol Rev 25:21–39

Perez-Ibarra I (2008) Aspectos sociales y culturales de la conservación de especies: el caso de la tortuga mora en el Sureste Ibérico. Ecosistemas 17:160–165

Pleguezuelos JM, Márquez R, Lizana M (eds) (2004) Atlas y Libro Rojo de los anfibios y reptiles de España. Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid

Real R, Pleguezuelos JM, Fahd S (1997) Distribution patterns of reptiles in the Riff region, Northern Morocco. Afr J Ecol 35:312–325

Real R, Barbosa AM, Vargas JM (2006) Obtaining environmental favourability functions from logistic regression. Environ Ecol Stat 13:237–245

Real R, Márquez AL, Estrada A et al (2008) Modelling chorotypes of invasive vertebrates in mainland Spain. Divers Distrib 14:364–373

Real R, Barbosa AM, Rodríguez A et al (2009) Conservation biogeography of ecologically interacting species: the case of the Iberian lynx and the European rabbit. Divers Distrib 15:390–400

Real R, Márquez AL, Olivero J et al (2010) Species distribution models in climate change scenarios are still not useful for informing policy planning: an uncertainty assessment using fuzzy logic. Ecography 33:304–314

Schumacher J (2006) Selected infectious diseases of wild reptiles and amphibians. J Exot Pet Med 15:18–24

US Geological Survey (1996) GTOPO30 Land processes distributed active archive center. (http://edcdaac.usgs.gov/gtopo30/gtopo30.asp)

Whittaker J (1984) Model interpretation from the additive elements of the likelihood function. Appl Stat 33:52–64